

Homoplasy and Adaptation in the Atelid Postcranium

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ABSTRACT Homoplasy is a ubiquitous phenomenon in phylogenetic investigations, but it is rarely investigated on its own. As a case study in the pattern and basis of homoplasy in primates, the atelid postcranium is discussed here. Characters available from Ford's ([1986] in Erwin J, Swindler DR, eds: *Comparative Primate Biology I: Systematics, Evolution, and Anatomy* (New York: Alan R. Liss), p 73–135; [1994] in Fleagle JG, Kay RF, eds: *Anthropoid Origins* (New York: Plenum Press), p 595–674) analyses of New World monkeys are mapped onto alternative phylogenetic trees for the family Atelidae to contrast patterns of character evolution and to develop explanatory hypotheses for differences in the trees. In an unrooted phylogenetic network, pitheciines do not group together because those pitheciines that routinely adopt hind limb suspensory postures (*Chiropotes*, *Cacajao*) share traits with atelines. Ford's (1986) work on phylogeny has shown that these traits are homoplastic and also identified potential synapomorphies of a clade comprised of modern pitheciins and atelines. However, following that work, congruence between studies of craniodental and molecular data suggested a still broader definition of atelids (including *Callicebus* and *Cebupithecia*), and in this case only one trait may define atelids, and several traits arise in parallel. The homoplastic characters in this phylogeny suggest that the phylogenetic signal in this set of postcranial data is overwhelmed by parallel adaptations to the use of climbing behaviors in all of Ford's atelids and suspensory postures in a more restricted set of taxa. These parallelisms probably indicate a bias of selective pressures in the South American environment, especially given the frequent, independent evolution of suspensory mammals there. This highlights the fact that homoplasy can be a dominant source of similarity in data partitions strongly influenced by a particular behavioral regime, in this case positional behavior. *Am J Phys Anthropol* 108:459–482, 1999. © 1999 Wiley-Liss, Inc.

All phylogenetic trees are characterized by some amount of homoplasy, or similarity among taxa that has arisen independently. One of the principles of parsimony in phylogenetic analysis is that homoplasy, though often very common, can never be abundant enough to warrant the choice of a less parsimonious phylogenetic tree (e.g., Farris, 1983). This logic presumes that homoplasy is distributed randomly; biases in the data can lead to patterned homoplasy that sup-

ports a false phylogenetic signal. For example, if development or structural relationships constrain the range of potential morphology, parallel selection is likely to evoke similar, homoplastic change. This com-

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bination of constraint and selection potentially interferes with phylogenetic analysis, as has been pointed out in many different situations (Alberch, 1989; Saether, 1979, 1983; Sluys, 1989; Wake, 1991; Wake and Larson, 1987). Parallel selection will most often occur if members of clades occupy similar environments or selective regimes.

When certain characters appear to repeat themselves within clades, the result is sometimes given a positive connotation and the repetition taken to mean that clade members share a potential for these characters (e.g., Cronquist, 1963; Brundin, 1972; Saether, 1977, 1979, 1983; Cantino, 1985; Sluys, 1989). Such a homoplastic trait is shown in Figure 1 and may be referred to as an underlying synapomorphy (Tuomikoski, 1967; Brundin, 1972; Saether, 1977, 1979) to recognize that its distribution implies the onset of a propensity to evolve the character. The term is explicitly intended to recognize a developmental potential that can, in a sense, arise like any other character. However, authors such as Saether (1977, 1979) recognized that external factors, such as environmental bias, can produce very similar patterns. In fact, where patterns consistent with the theoretical prediction of underlying synapomorphies have been found, the role of selection has been stressed (Brooks and McLennan, 1991; Bell et al., 1993; DeSalle and Grimaldi, 1993; Brooks, 1996). It is also clear that in these cases the pattern of homoplasy does not automatically imply a particular process.

There are two ways to show that homoplasy is patterned in a meaningful way. One is to evaluate trait distributions in a statistical sense—in other words, to ask whether clades show tendencies to repeat certain character transformations. Sanderson (1991) did this by determining the probability that instances of repeated character evolution within four taxa of various ranks (*Astragalus* (a legume), Iguanidae (a squamate), Asteraceae (angiosperm), and Amniota) could be replicated in randomized phylogenies. He concluded that fewer than 5% of the characters showed statistically significant tendencies in any of the groups and that therefore the null hypothesis of randomly distributed

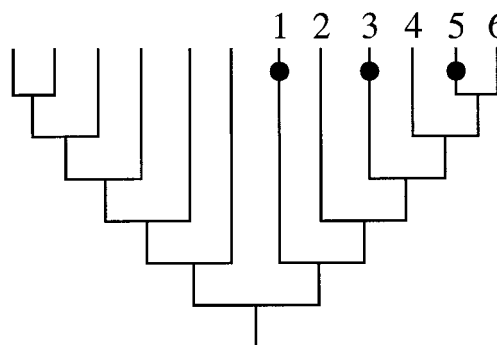


Fig. 1. An example of a character that shows patterned homoplasy. Taxa in the clade on the right side arguably have a tendency to evolve the character (filled circle) independently.

homoplasy could not be rejected. At the same time, however, Sanderson (1991:357) pointed out that all characters would show statistically significant patterns at some level, because the organisms in the outgroup are "so different that the *requisite underlying form* is not present" (emphasis added). This statement is in essential agreement with those that believe the requisite underlying form actually contributes to parallel evolution, and therefore Sanderson (1991) suggested that more inclusive studies might better reveal patterned homoplasy. It must also be recognized that some obviously homoplastic traits are routinely omitted from data sets intended for phylogenetic analysis, such as those used by Sanderson (1991).

The second way to evaluate patterned homoplasy is to focus on the discordance between phylogenies supported by different types of data, or data partitions (cf., Wray, 1996; Ward, 1997). That is the approach of this study. If a number of traits are homoplastic and have similar distributions in a data set, a phylogeny may result that is supported by traits that appear incorrectly to be synapomorphies. As an example, Wray (1996) demonstrated the dramatic effects of parallel evolution among echinoid larvae. So many characters are affected by independent, stepwise shifts to nonfeeding larvae that an analysis of larvae alone provides an estimate of phylogeny very different from that based on adult morphology and molecu-

lar data, essentially identifying a false clade of larval forms defined by similar behavior.

Patterned homoplasy, as in this example, invalidates the principle that misleading information should be randomly distributed in parsimony-based analyses of phylogeny. It may be that only data sets representing a limited data partition are subject to the problems of patterned homoplasy, for the reason that a data partition by definition reflects a particular expression of data and set of processes (Bull et al., 1993; Lanyon, 1993; Miyamoto and Fitch, 1995).¹ The theoretical basis for combining evidence from different sources of data (total evidence) is based on the premise that conflicting patterns of homoplasy will eliminate one another and that only the phylogenetic signal will be retained (e.g., Kluge, 1989; Barrett et al., 1991; Chippindale and Wiens, 1994). Even though many authors do not favor combining characters from different data partitions (Bull et al., 1993; Miyamoto and Fitch, 1995), it is a widely accepted principle that multiple lines of evidence must be compared in some fashion to obtain the most probable phylogeny. However one incorporates different lines of evidence, a focus on character evolution within particular data partitions, combined with studies of functional morphology and observation of behavioral correlates, helps to develop hypotheses of homoplasy and adaptation (Brooks and McLennan, 1991; Wake, 1991; Brooks, 1996; Larson and Losos, 1996).

In New World monkeys, separate data partitions suggest different definitions of the family Atelidae and different patterns of evolution within it (see below). Craniodental traits appear to show strong patterns of parallel evolution within atelines (Rosenberger, 1979, 1992; Kay et al., 1987; Kay, 1990; Anthony and Kay, 1993; Horovitz and Meyer, 1997) but suggest a broader definition of the family than do the postcranial data (Ford, 1986). Several points of agreement have been found between craniodental data and the preponderance of genetic data

(Schneider et al., 1993, 1996; Horovitz and Meyer, 1997). In this study, I will focus on postcranial traits and to what extent patterns of homoplasy may explain the conflict between these traits and other data sets. Character evolution in the postcranium will be analyzed for three different reconstructions of platyrrhine phylogeny: one based on an unrooted phylogenetic network (estimated here), one incorporating an outgroup (taken from Ford, 1986), and one constructed from the points of agreement among several analyses of platyrrhine phylogeny. The latter is regarded as the phylogenetic tree that best reflects as much of the available data as possible. I will evaluate the patterns of homoplasy in each tree with respect to issues of character definition, such as their independence, and patterns of positional behavior in New World monkeys will be drawn on to provide explanatory hypotheses for the homoplastic traits.

PLATYRRHINE PHYLOGENY

Within primates, platyrrhines provide a useful study group for the investigation of homoplasy because the infraorder is almost assuredly monophyletic, and independent reconstructions of platyrrhine phylogeny are available based on craniodental (Rosenberger, 1979, 1981, 1992), dental (Kay, 1990), and postcranial (Ford, 1986) lines of evidence² as well as sequence data from two nuclear genes (IRBP Intron 1 and ϵ -Globin) (Schneider et al., 1993, 1996; Harada et al., 1995). Recently Horovitz and Meyer (1997) have performed an analysis combining evidence from nuclear gene sequences (Schneider et al., 1993; Harada et al., 1995) with a sequence from the mitochondrial 16S ribosomal gene (Horovitz and Meyer, 1995) and a set of mostly craniodental morphological characters. See Table 1 for definitions of taxonomic terms used in this paper.

Platyrrhine phylogenies have generally been based on cladistic methodology, with the exception of Rosenberger (1979, 1981,

¹To what extent data partitions are natural classes of data is a debatable issue (Nixon and Carpenter, 1996; Desalle and Brower, 1997).

²Ford (1986) incorporated multiple types of data, but some craniodental characters were missing data for many taxa, and in any case postcranial morphology was the dominant source of information. Only postcranial data are considered in the present study.

TABLE 1. Classification adopted here for the New World monkeys¹

Infraorder Platyrrhini
Family Atelidae
Subfamily Atelinae
Tribe Atelini
<i>Ateles</i> , <i>Brachyteles</i> , <i>Lagothrix</i>
Tribe Alouattini
<i>Alouatta</i>
Subfamily Pitheciinae
Tribe Pitheciini
<i>Cebupithecia</i> , ² <i>Pithecia</i> , <i>Chiropotes</i> , <i>Cacajao</i>
Tribe Callicebini
<i>Callicebus</i>
Family Cebidae
Subfamily Aotinae
<i>Aotus</i>
Subfamily Cebinae
<i>Cebus</i> , <i>Saimiri</i>
Subfamily Callitrichinae
<i>Callimico</i> , <i>Saguinus</i> , <i>Leontopithecus</i> , <i>Cebuella</i> , <i>Callithrix</i>

¹ This classification follows Schneider et al. (1993, 1996) and Meldrum and Kay (1997). Only genera discussed in this study are listed. Note the difference between informal terms for subfamilies and tribes: *ateline* and *atelin*, as well as *pitheciine* and *pitheciin*.

² Fossil taxon.

1992). While adopting the tenets of phylogenetic systematics with regard to the importance of polarity, Rosenberger defined clades based on adaptive zones and modalities. For example, he attributed the initial split between cebids and atelids to masticatory differences, as expressed in the following:

Cebids emphasize premolar puncture-crushing mastication and show relatively reduced molar crushing-grinding abilities, suggesting a frugivorous-insectivorous dietary habit. The atelids possibly favor molar mastication and appear to have a feeding system geared to heavy-duty processing by the posterior teeth. Within these zones, sublineages diversified to embrace separate adaptive modalities. (Rosenberger, 1979:vi)

Further explanation is available in Rosenberger (1992). Rosenberger (1979) acknowledged that atelids are not defined by any synapomorphies for which the polarity is clear. The potential synapomorphies are a reduced buccal cingulum, enlarged hypodons, a closed glenoid fossa, and a ventral slope to the inferior border of the mandibular corpus. Kay (1990) pointed out that they could well be primitive for platyrrhines based on their distribution in nonatelid platyrrhines and *Aegyptopithecus*. In any case, it is apparent that Rosenberger's phylogenetic tree does not rely on a preponderance of shared-derived characters to link taxa but

rather an emphasis on key characters or behavior that may reveal unique adaptive trends. In effect, defining clades in this way is a strong form of character weighting.

No postcranial characters were listed by Rosenberger as characteristic of atelids. This resulted in part because of his focus on craniodental morphology but also because the inclusion of *Aotus* and *Callicebus* in Atelidae made the family substantially more heterogeneous in postcranial morphology. Ford's (1986) work, based mainly on postcranial evidence, excluded these taxa from atelids. Instead, she concluded that atelines and extant pitheciins (*Pithecia*, *Chiropotes*, *Cacajao*) form a clade that is the sister group to atelines. This more limited version of atelids was characterized by 12 postcranial state changes and thus well supported by that data set.

A critical taxon not discussed above is *Cebupithecia*, a Miocene platyrrhine widely thought to be a basal pitheciine based on dental evidence (Stirton and Savage, 1951; Rose and Fleagle, 1981; Ford, 1990; Kay, 1990; Kinzey, 1992; Meldrum and Kay, 1997). The phylogenetic position of *Cebupithecia*, in combination with its unusual combination of primitive and derived postcranial features, has already called attention to homoplasy in the atelid postcranium (Ford, 1986, 1990; Meldrum and Lemelin, 1991; Meldrum, 1993). The present study explores patterns in greater detail and with added reference to *Callicebus*.

POSITIONAL BEHAVIOR IN ATELIDS

Positional behavior is not the only sphere of behavior for which postcranial morphology may be adapted, but it is the predominant one. Therefore, to develop causal explanations of patterns of homoplasy within atelids and to judge the adaptive meaning of homoplastic characters, I will review positional behavior in atelids and other platyrrhines. Different recording methodologies and different categorical definitions mean that comparisons among studies are not always straightforward. I will focus on those categories of behavior that are considered to be important in discussing atelid adaptation. These are suspension and climbing and, for *Pithecia*, leaping.

With suspension, it is important to separate locomotion from posture, particularly feeding posture. Suspension is a substantial part of locomotion only in atelins among platyrrhines. The best documentation of this is for *Ateles* (Mittermeier and Fleagle, 1976; Mittermeier, 1978; Cant, 1986; Fontaine, 1990). Results from Cant (1986) and Fontaine (1990) both indicate that suspension (mostly bimanual) makes up around 25% of *Ateles* locomotion. Less detailed accounts of *Brachyteles* (e.g., Nishimura et al., 1988) suggest a similar pattern to *Ateles*, while the importance of suspension in *Lagothrix* locomotion appears to be less than in the other taxa (Fleagle, 1988; Ramirez, 1988). In contrast to the atelins, *Alouatta* engages in very little suspensory locomotion (Mendel, 1976; Cant, 1986; Gebo, 1992). In this respect, it is like other platyrrhines.

The use of suspensory postures during foraging and feeding is more widespread in platyrrhines and most apparent in atelines, *Cacajao*, *Chiropotes*, and *Cebus*. The prehensile tail is a critical component of suspensory postures in atelines (e.g., Mittermeier, 1978; Cant, 1986; Fontaine, 1990) and *Cebus* (Garber and Rehg, 1997). Cant (1986) and Fontaine (1990) found that, among several different kinds of suspensory postures, tail-only suspension is the most frequent in *Ateles geoffroyi*. These results differ somewhat from those of Mittermeier (1978), who observed that both *Ateles geoffroyi* and *Ateles paniscus* most often use two limbs and the tail in suspension. It appears in each study of *Ateles* that the hind limbs play a weak suspensory role. Detailed quantitative data are lacking for *Brachyteles* and *Lagothrix*. However, from the various qualitative accounts of these atelins (Nishimura et al., 1988; Ramirez, 1988; Fleagle, 1988), it is fairly clear that *Ateles*, *Brachyteles*, and *Lagothrix* have a greater ability to use only the prehensile tail in suspension than do other platyrrhines. When used, other limbs are often oriented irregularly and used for stability while abducted.

Suspensory postures account for almost all nonsitting postures during *Alouatta* feeding (Mendel, 1976; Schön Ybarra, 1984; Bicca-Marques and Calegario-Marques, 1993). In contrast to *Ateles*, *Alouatta* fre-

quently incorporates its hindlimbs into suspensory postures (Schön Ybarra, 1984; Cant, 1986).

Alouatta is thus somewhat intermediate between *Ateles* and those pitheciins that engage in suspensory postures, *Chiropotes* and *Cacajao*. In the latter, suspension is usually hindlimb suspension and predominantly used for feeding in terminal branches. The only quantitative data for this behavior are from Walker and Ayres (1996), with frequencies of 1.2% in *Chiropotes* and 3.5% in *Cacajao calvus* (of all feeding time). These numbers appear quite small at first glance. However, Walker and Ayres (1996) used instantaneous sampling, which minimizes the recognition of activities with short duration. They also note that *Cacajao* spends more feeding time in locomotion than do other pitheciins. This locomotion is not only the task of searching out more food but the significant component of foraging/feeding in which the animal moves back and forth between terminal branches, where it obtains fruit, to stable supports closer to the center of the tree, where it actually consumes the food (see also Fontaine, 1981). Given this amount of movement, it is not surprising that even a critical activity such as suspension from terminal branches would have poor representation as a percentage of overall time. A better question for *Cacajao* is, during what percentage of feeding bouts does the animal use hindlimb suspension at all? Qualitative descriptions suggest that this is moderately high (Fontaine, 1981; Fleagle and Meldrum, 1988; Walker and Ayres, 1996).

Walker and Ayres (1996) do not provide details on *Chiropotes* feeding strategy that permit evaluation of the importance of hindlimb suspension in feeding, but other reports suggest it is a significant method of foraging (van Roosmalen et al., 1981, 1988). The frequencies of suspension reported by Walker and Ayres (1996) for *Chiropotes* are similar to those of *Cebus capucinus* provided by Gebo (1992) but lower than those in Garber and Rehg's (1997) study of *Cebus*.

The primary difference between pitheciins that engage in suspension and the atelines (or *Cebus*) is that the latter have prehensile tails which can be used for sus-

pension alone or in combination with other limbs. The prehensile tail enhances the atelines' ability to consume food or rest while suspended, leading to a different style of foraging than *Cacajao* and much higher frequencies of suspensory postures, even though *Cacajao* frequently resorts to hindlimb suspension for short periods during feeding. Gross categorization of the importance of suspension in foraging and feeding would suggest that *Chiropotes* is the most infrequent user of suspension, *Cacajao*, *Cebus*, and *Alouatta* somewhat more frequent users, and the atelins the most frequent users. Atelins also show the greatest emphasis on tail-hanging.

Thus, not all atelids make substantial use of suspensory postures. In particular, these behaviors occur very rarely in *Pithecia* (Walker, 1996; Walker and Ayres, 1996) and *Callicebus* (Kinzey, 1976, 1981). However, it should be added that Walker's (1996) results are somewhat at odds with earlier, informal reports of hindlimb suspension in *Pithecia* (Sanderson, 1957; Buchanan et al., 1981; see also the review by Stern, 1971).

Data are generally lacking on suspensory postures in callitrichines. Boinski (1989) recorded suspensory postures in *Saimiri*, finding a frequency of roughly 2%. Garber and Pruett (1995) observed frequencies of 1–3% for prehension in *Saguinus mystax*. It is likely that many other platyrrhines show similar percentages. Therefore, to regard hind limb suspension as a critical behavior in genera such as *Chiropotes* and *Cacajao* relies to some extent on anecdotal reports by several authors that it is frequently important in foraging behavior, not on obviously elevated frequencies of quantitative data.

Another important aspect of positional behavior in atelids is climbing. Climbing is a frequent component of locomotor behavior in all pitheciins, atelines, and *Cebus*, but this statement requires careful definition. Different views of what constitutes climbing have led to variable results for the same taxa. The key issue is whether climbing is restricted to vertical movements or also includes horizontal and oblique movements through multiple, irregular substrates. The latter movement, clambering, differs from quadrupedalism in lacking a consistent gait

pattern and requiring more pronounced limb abduction. Studies of New World monkeys that have restricted climbing to vertical motion include Mittermeier and Fleagle (1976) and Fontaine (1990), while other studies have used the broader definition (Fleagle and Mittermeier, 1980; Schön Ybarra and Schön, 1987; Gebo, 1992). Walker and Ayres (1996) separated out both climbing and clambering. In their definition, vertical climbing took place only on substrates oriented at more than 70° to the horizontal. The justification for using any kind of clambering rather than just vertical climbing is that the demands for joint mobility are similar, and both behaviors represent a departure from obligate arboreal quadrupedalism and its more stereotyped range of limb motion.

A general proclivity for climbing is clear in *Ateles*, but for this genus definitions have varied substantially among studies. Cant (1986) concluded that 52% of *Ateles* locomotion was quadrupedal walking, but he used no climbing category. Pronograde clamber was treated as a distinct category (9% of travel), but vertical climbing was subsumed into quadrupedal walking, which was taken to mean locomotion using four limbs on supports of any orientation. Therefore, the total proportion of locomotion that involved travel across irregular substrates of any orientation is something greater than 9%. An analogous problem in interpretation occurs with Fontaine's (1990) data. He did not separate pronograde clambering from other kinds of quadrupedalism, and climbing was restricted to various kinds of vertical travel. The different kinds of vertical climbing together represent 9% of *Ateles* locomotion. Again, the inference is that travel across multiple, irregular substrates is substantially greater than 9%.

Gebo (1992:279) recorded data on positional behavior in both *Alouatta* and *Cebus* using a climbing definition that incorporated clambering through "irregular and intertwined small supports." These frequencies are 37% in *Alouatta* and 26% in *Cebus*, with locomotion and foraging/feeding pooled in both cases.

The pivotal taxon for generalizations about atelid climbing behavior is *Pithecia*. Fleagle

and Mittermeier (1980), followed by Fleagle and Meldrum (1988), found that leaping dominates the locomotor bouts of *Pithecia pithecia* and that only 5% of bouts were climbing (based on small samples). Nonetheless, they regarded the climbing behavior as important relative to its use in nonatelid platyrrhines.

A later study of the same species took place in a different habitat and used different methodology. Walker (1996; Walker and Ayres, 1996) observed a low frequency of vertical climbing (2.1%), but, when all categories representing quadrumanous travel across multiple, irregular substrates are subsumed, the Walker (1996) data give a total of 18.7% in *Pithecia*. Climbing/clambering therefore does appear to be a significant proportion of *Pithecia* locomotion, and this pooled category gives a similar result for *Chiropotes* (21.4%) and *Cacajao* (25.5%). In fact, the ranking of pitheciine taxa in this category is the same as the use of hind limb suspension during feeding.

In his description of *Callicebus* locomotion and posture, Kinzey (1976, 1981) made no mention of vertical climbing or clambering, suggesting that the positional repertoire of *Callicebus* is mainly arboreal quadrupedalism interspersed with deliberate leaps between horizontal supports. On some occasions, particularly in foraging/feeding behavior, *Callicebus* clings to vertical supports or leaps between them.

Field observations on both *Saguinus* (Garber, 1991; Castro, 1991; Garber and Pruetz, 1995) and *Saimiri* (Fleagle and Mittermeier, 1980; Boinski, 1989; Fontaine, 1990) show that these taxa rarely climb, by any definition. Still, it must be noted that the difference between these taxa and atelids is one of frequency of climbing, not of presence or absence. *Saguinus* engages predominantly in quadrupedalism and quadrupedal leaping, with climbing (including clambering) representing 1–12% of locomotion during travel depending on the population studied. The vast majority of *Saimiri* locomotion is quadrupedalism, with climbing representing approximately 3–4% of locomotor behavior. Definitions used by Boinski (1989) imply that *Saimiri* does not engage in clambering

behavior and that climbing, when it does rarely occur, is vertical.

Finally, the positional repertoire of *Cebupithecia* will never be observed, but it is probable that *Cebupithecia* rarely climbed, instead combining quadrupedalism with leaping behavior (Ford, 1990; Meldrum, 1993).

In sum, among positional behaviors important for understanding adaptation in atelids, climbing is a relatively important form of locomotion in *Cebus* and all extant atelids except *Callicebus*. Suspensory postures are an important component of feeding behavior in *Cebus*, *Chiropotes*, *Cacajao*, and the atelines. Suspensory locomotion is rare outside of the atelins, particularly *Ateles* and *Brachyteles*. Other platyrrhines rarely climb or suspend, but, given the relative lack of data on their positional behavior, this statement remains tentative.

METHODS

The approach used here to examine homoplasy is to study character evolution for three different phylogenetic trees of atelids, each of which reflects a different set of assumptions. It will be noted to what extent the patterns of homoplasy change depending on the assumptions made and how these relate to the probable acquisition of positional behaviors discussed above.

Data

The data set used in this study is taken from Ford's work (1986, 1994) and is described in Table 2 and the appendix. As in Ford (1986), polymorphic taxa are treated as possessing their own character states, but for some characters the states have been renumbered for ease of interpretation. In some instances, two characters from Ford (1986) are combined into a single character (following Ford [1994]). For instance, character 41 is a combination of both PC117 and PC118 of Ford (1986), the form of the deltopectoral crest.

My criteria for selecting a subset of characters from Ford's (1986) database are based first on whether Ford (1994) used the trait in her more limited data set. Her two studies differed in several ways. Most importantly, Ford (1994:598) excluded what she consid-

TABLE 2. Character state distributions¹

	Characters																																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	
Ancestral states	3	1	1	1	1	0	0	0	0	1	1	0	1	0	1	3	0	0	1	0	0	1	1	0	0	0	1	2	0	0	0	1	0	0	1	2	0	4	2	0	2	0	2	1
<i>Cebus</i>	3	1	1	1	1	1	0	0	1	1	1	0	3	3	1	3	1	1	1	0	0	4	1	0	0	3	2	0	0	2	1	0	1	1	2	0	4	4	0	0	2	2	1	
<i>Saimiri</i>	4	2	1	0	2	0	0	0	0	1	1	1	2	2	1	1	1	0	1	2	4	2	1	3	0	1	3	1	0	2	1	0	0	1	2	0	2	3	1	2	1	3	1	
<i>Aotus</i>	2	1	1	1	2	0	0	0	0	2	2	0	2	2	1	3	1	0	2	2	3	1	1	3	1	0	2	0	0	0	1	0	0	1	1	1	3	1	2	3	1	4	1	
<i>Callicebus</i>	1	2	2	1	1	1	0	0	0	1	1	0	2	0	1	3	0	0	1	2	4	1	1	3	0	1	1	0	0	0	1	1	0	1	2	2	1	2	1	2	1	4	1	
<i>Callimico</i>	3	1	2	2	0	0	0	0	1	1	2	4	2	3	1	1	2	1	1	2	4	1	1	4	2	2	2	1	0	0	2	0	0	0	2	0	5	2	3	4	0	2	2	
<i>Leontopithecus</i>	3	1	2	1	0	0	0	0	1	1	1	4	2	3	1	1	2	1	0	2	4	1	1	4	1	2	3	1	0	1	2	0	0	0	2	2	2	3	3	3	0	4	2	
<i>Saguinus</i>	3	1	1	1	0	0	0	0	1	1	2	3	1	3	1	1	1	1	0	2	4	1	1	4	1	3	2	0	0	0	1	0	0	1	2	1	5	2	0	0	0	4	2	
<i>Callithrix</i>	3	0	2	1	0	0	1	0	1	1	2	3	2	3	1	2	2	1	0	2	4	1	0	4	1	3	2	1	0	0	1	0	0	0	1	2	6	1	1	4	0	4	2	
<i>Cebuella</i>	4	0	2	1	0	0	0	0	1	1	2	3	1	3	1	1	2	0	0	3	4	1	0	4	1	3	2	0	0	0	1	0	0	1	0	2	6	0	1	4	0	4	2	
<i>Pithecia</i>	3	2	2	2	2	0	1	0	0	1	2	1	2	2	1	1	0	1	1	2	1	2	0	2	0	3	0	0	0	0	0	3	1	1	2	0	5	3	3	4	1	1	1	
<i>Chiropotes</i>	4	2	1	1	2	0	0	0	0	1	2	0	3	0	1	1	0	1	1	2	1	4	2	0	0	3	1	0	0	2	0	2	1	2	2	0	1	4	3	2	2	0	0	
<i>Cacajao</i>	3	2	2	1	2	1	1	0	0	1	2	2	3	0	0	1	0	0	2	0	3	1	1	1	1	3	0	0	1	2	0	2	1	2	2	0	3	3	3	3	2	0	1	
<i>Alouatta</i>	3	1	2	4	1	2	0	1	0	0	2	4	4	0	0	0	0	2	0	2	2	4	1	1	1	2	2	1	2	2	1	2	2	2	1	2	3	3	0	1	1			
<i>Lagothrix</i>	5	2	1	4	2	2	1	1	0	0	2	4	4	0	0	0	0	1	0	0	1	3	2	0	2	3	3	2	1	2	3	2	1	2	2	2	4	3	3	4	3	1	2	
<i>Ateles</i>	5	0	1	4	1	2	1	1	0	0	2	4	4	0	0	0	0	2	0	0	1	4	1	0	2	3	2	2	1	2	3	1	1	2	2	2	2	2	3	4	3	1	2	
<i>Brachyteles</i>	5	0	2	4	0	2	1	1	0	0	2	4	4	0	0	0	0	2	0	0	4	4	2	0	0	4	1	1	2	2	1	2	1	3	2	2	1	1	3	4	3	1	2	
<i>Cebupithecia</i>	3	0	2	3	2	0	0	1	0	1	2	2	3	1	1	0	0	0	1	1	4	0	1	0	?	2	2	1	0	0	?	2	1	1	?	0	6	2	1	1	1	2	0	

¹ See the appendix for character definitions.

ered to be "the most variable characters and those that were clearly primarily the result of size differences (allometry)." In all, 47 characters were used in both works. Of these, three are excluded here because they do not vary among platyrrhine genera according to the 1986 character state distribution (angle of posterior articular surface to long axis of calcaneus [Ford PC28], width of posterior articular facet relative to maximum length of cuboid articular surface on the calcaneus [Ford PC34/35], and length of posterior calcaneus relative to maximum length of cuboid articular surface [Ford PC32]). The size of the peroneal tubercle (Ford PC1/2/3) is excluded because in both of Ford's studies it is also coded to reflect extremely complex patterns of polymorphism and is not amenable to interpretation as a synapomorphy or parallelism. Therefore, 43 postcranial traits are included in this study. All characters are of the calcaneus, tibia, femur, or humerus. These traits are not intended to represent the postcranium exhaustively.

Selection of phylogenetic trees

The three phylogenetic trees used to study character evolution are an unrooted network, Ford's (1986) hypothesis of phylogeny, which represents the most parsimonious interpretation of this data set once probable ancestral states are incorporated, and a composite phylogenetic tree that is preferred here.

The unrooted network essentially involves no assumptions about polarity or the ordering of character transformations (*network* is simply the correct term for an unrooted cladogram). In comparison with phylogenetic trees, this will provide some information on how rooting affects interpretation of the data set. The network was estimated using PAUP 3.1 (Swofford, 1993). Characters are left unordered. The heuristic swapping branches option was used with four starting trees, those published by Rosenberger (1979), Ford (1986), Kay (1990), and Schneider et al. (1996). Test runs of various subclades within platyrrhines, including one with atelids alone, consistently gave the same result whether trees were searched using an exhaustive branch-and-bound

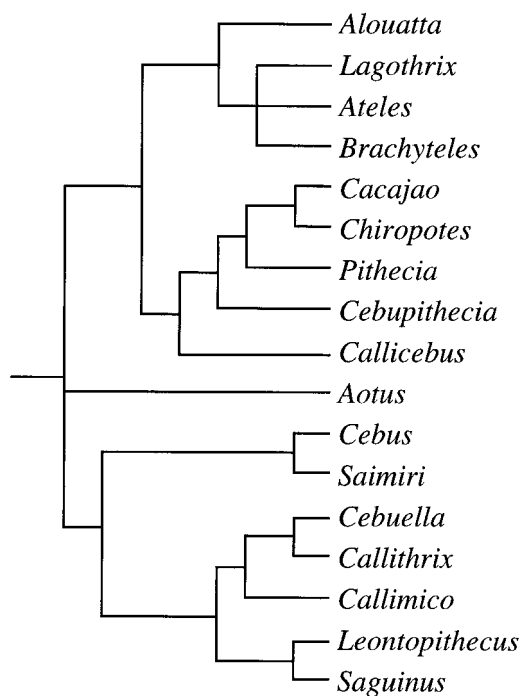


Fig. 2. A phylogeny used here to represent the more strongly supported points in atelid evolution, as discussed in the text. This is mainly derived from Rosenberger's (1979) phylogenetic tree based on craniodental data, Schneider et al.'s (1996) tree based on nuclear gene sequences, and the position of *Cebupithecia* discussed by Kay (1990), Kinzey (1992), and Meldrum et al. (1997). The position of *Aotus* is left unresolved with respect to the two major clades, and within-atelid relationships are unresolved, reflecting the lack of agreement among phylogenetic analyses (but see the combined analysis by Horowitz and Meyer, 1997).

search or whether the swapping branches heuristic option with the same starting trees was used.

The strict consensus tree of this analysis was first determined. Characters were then reweighted according to their respective maximum consistency indices among the equally parsimonious trees (a form of successive weighting [Farris, 1969]), and the phylogeny was reestimated. Both types of results are given below.

The composite phylogenetic tree used here is intended to reflect the points of agreement among different data partitions relevant to platyrrhine evolution. It is shown in Figure 2 and is constructed from the four main alternative phylogenies of platyrrhines (Rosenberger, 1981; Ford, 1986; Kay, 1990;

Schneider et al., 1996; see also Schneider and Rosenberger, 1996; Horovitz and Meyer, 1997; Meldrum and Kay, 1997) as well as studies of the fossil taxon *Cebupithecia*. These phylogenetic trees have been estimated from essentially independent data or methodology, with those of Rosenberger (1981) and Kay (1990) overlapping most strongly in the type of data (but not the conclusions).

First, all studies agree on the membership of monophyletic clades Atelinae and extant Pitheciini (*Pithecia*, *Chiropotes*, *Cacajao*), with *Pithecia* being the most primitive extant pitheciine. *Alouatta* was found to be the sister group of other atelines by all authors except Kay (1990), who expressed doubts about this particular aspect of his phylogeny (see also Kay et al., 1987; Horovitz and Meyer, 1997).

Furthermore, Pitheciini includes the Miocene fossil taxon *Cebupithecia* as its basal member (Stirton and Savage, 1951; Rose and Fleagle, 1981; Ford, 1990; Kay, 1990; Kinzey, 1992; Meldrum and Kay, 1997). Unlike other aspects of the phylogeny in Figure 2, the position of *Cebupithecia* does not reflect agreement between any two or more data sets; rather, it represents the collective view that the unique dental features shared by *Cebupithecia* and the pitheciines are of stronger weight than the postcranial features that conflict.

With respect to atelids, the only other agreements are the conclusions reached by Rosenberger (1981) and Schneider et al. (1996) that the sister group to atelids is a monophyletic cebid group and that *Callicebus* (tribe Callicebini) is in the sister group to the pitheciins. In other aspects of phylogeny, there is no independent support for any particular relationship. The position of *Aotus* varies dramatically among studies, but it is generally held not to be an atelid (contra Rosenberger, 1979). Postulated relationships within atelins (*Brachyteles*, *Lagothrix*, *Ateles*) are currently too discordant to resolve what are the most likely relationships.

Recently Horovitz and Meyer (1997) have favored a phylogeny based on combined data sets that is very similar to that in Figure 2, except that their tree resolves the position of *Aotus* at the base of the nonatelid clade and

suggests a sister group relationship of *Brachyteles* and *Lagothrix*. These results are derived from combining characters from different data sets. Horovitz and Meyer (1997) also performed an analysis of morphology alone (mainly craniodental data) that follows Rosenberger (1979, 1981) in the position of *Callicebus* and Kay (1990) in the sister group relationship of *Brachyteles* and *Alouatta*. These results emphasize the position of *Callicebus* that is gaining wide acceptance (e.g., Meldrum and Kay, 1997). Like Kay (1990), Horovitz and Meyer (1997) concluded that the putative *Brachyteles* + *Alouatta* clade is not valid when all evidence is considered.

Character evolution

Characters are mapped onto the unrooted network, Ford's (1986) phylogenetic tree,³ and the composite tree for atelids (Fig. 2) in order to determine patterns of homoplasy in each case. For this section, characters are optimized onto the trees using the DELTRAN procedure in PAUP (Fig. 3). When faced with a character whose distribution suggests either an early change followed by reversal at a more terminal node or parallel changes in the taxa showing the character state in question, the DELTRAN method prefers the latter. Note that, as is typical of many primate phylogenies, very few of these reconstructed changes represent true synapomorphies (i.e., derived character states shared by all members of a defined clade). Instead, further changes often take place in more derived taxa (Ford, 1994).

A hypothesis of character evolution such as the DELTRAN procedure is necessary for illustrative purposes because some characters (the minority) change in ambiguous positions on the tree, but they demonstrate homoplasy—either parallelisms or reversals to the ancestral state—in any reconstruction of their evolution. How this technique affects the interpretation of some characters is discussed below. Only to show unambiguous changes would discard relevant information on homoplasy.

³Note that the difference between the unrooted network and Ford's (1986) phylogeny does not reflect differences in the data set. For atelids, the more limited data set used here reproduces Ford's (1986) result if her ancestral states are used for rooting.

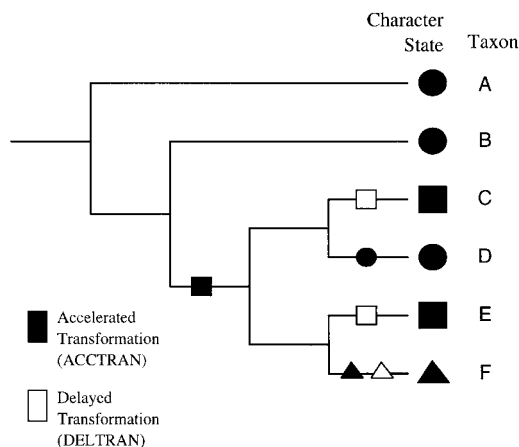


Fig. 3. Reconstructing character evolution. PAUP 3.1 (Swofford, 1993) contains two different methods of character evolution: accelerated transformation, preferring gains followed by reversals, and delayed transformation, preferring parallel gains. Which of these models is more often accurate has not been determined for one character. The example above illustrates how the methods differ. Where the methods coincide (here leading to taxon F), character state changes are called unambiguous. For other (ambiguous) changes, delayed transformation is used here for illustrative purposes, with the understanding that a different model could validly be used.

To determine the most important patterns of homoplastic traits in this data set, I will focus on the character states unique to atelids. Homoplastic traits that are unique to a particular clade are arguably the surest signal of developmental and/or environmental constraints.

RESULTS

Estimation of unrooted network

An unrooted network is estimated for comparison with Ford's (1986) rooted phylogeny in order to determine the effect of her ancestral states. Two unrooted networks of length 199 are equally parsimonious for platyrrhines using the 43 characters included here; the strict consensus of these is shown in Figure 4a. This consensus tree is unresolved with respect to *Chiropotes* and *Cebus*. One of these networks is more favored using successive weighting by the consistency index (Fig. 4b). By definition, this network has no base, and therefore true clades are not identified unless a rooting is applied. Nonetheless, any rooting consistent

with this topology would make pitheciins, and therefore atelids as a whole, paraphyletic. *Chiropotes* and *Cacajao* are potentially in a monophyletic clade with the atelines. *Cebus* is the taxon adjacent to this clade.

Character evolution

Character state changes within the clade most inclusive of atelids (this varies among different trees) are shown on alternative reconstructions of phylogeny in Figures 5–7. These are the unrooted network estimated above, Ford's (1986) phylogenetic tree, and the composite tree. Homoplastic characters are discussed in the text below. In all of these figures, black or striped character state changes are homoplastic and unique to atelids, while other changes occur only once in platyrrhines as synapomorphies of various atelid subclades. The display of unique character states in this way mainly eliminates traits that are homoplastic throughout platyrrhines.

Unrooted network. Figure 5 shows the characters defining potential atelid subclades in the unrooted network. This pattern would result if the network were rooted anywhere outside this particular grouping and is used for heuristic purposes. *Chiropotes* is the most basal taxon in a clade defined by several character states unique to this clade, including a wide patellar groove (32:2), a femoral head that extends more proximally relative to the greater trochanter (34:2), and a rounded deltopectoral crest (42:0). The wide patellar groove and proximally positioned femoral head confer increased mobility to the hindlimb (Fleagle, 1983; Rose, 1983). Another character that indicates a mobile hindlimb defines the *Cacajao* + Atelinae clade in this tree. The anterior border of the trochlear facet on the tibia is flattened (15:0) as opposed to sharp. In addition, *Cacajao* is polymorphic for a curl of subchondral bone over the lateral margin of the patellar groove, as are some atelines (29:1,2; *Alouatta* and *Brachyteles* show character state 2, meaning most or all individuals lack the extension of subchondral bone).

The unrooted network places *Cebus* adjacent to *Chiropotes* because of several traits

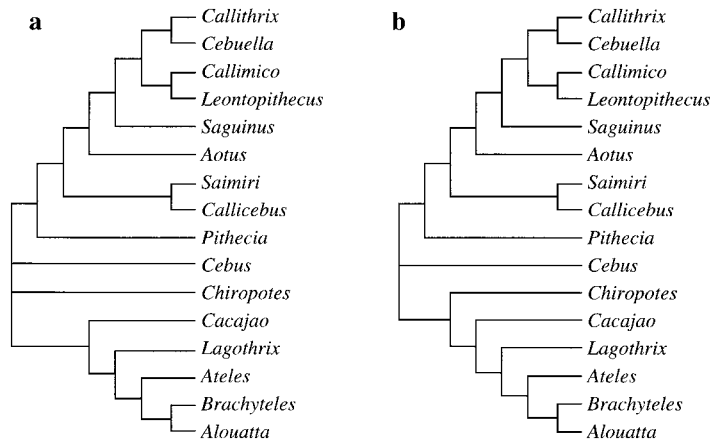
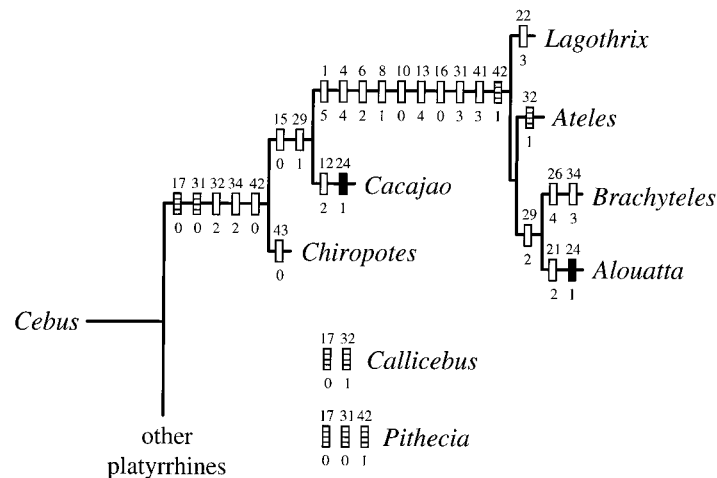


Fig. 4. Unrooted networks. Two networks of length 199 steps are equally parsimonious for platyrrhines using the 43 characters included here. They differ in the relative positions of *Cebus* and *Chiropotes*. Shown here are (a) the strict consensus of these and (b) the favored network when characters are reweighted by their maximum consistency indices from the two networks.

Fig. 5. Occurrence of character states unique to the subset of atelids depicted here as a clade. Dark blocks indicate homoplastic changes. In addition, convergences with *Callicebus* and *Pithecia* are shown by striped blocks. Character number is listed above, state number below. Phylogenetic tree derived from Fig. 4b.



(13:3, 22:4, 24:0, 41:2), but these are quite variable among atelids. The main instances of homoplasy in the atelid clade result because of the position of *Pithecia*. They are the following convergences between *Pithecia* and the *Chiropotes* + *Cacajao* + Atelinae clade: no horizontal groove on the posterior surface of the tibial malleolus (17:0) and a distally placed third trochanter (31:0).

Phylogenetic tree from Ford (1986). With *Pithecia* as the basal member of a monophyletic Pitheciini that is the sister group to Atelinae, as in Ford (1986), there are three reconstructed character state changes that define the atelids (Fig. 6). A rounded deltopectoral crest (42:1) and a relatively broad patellar groove (32:2) are unique to atelids among platyrrhines. A

broad distal epiphysis of the femur (33:1; not illustrated) is shared also with *Cebus*. For two of these traits, further changes take place, but these are not reversals. The deltopectoral crest is more rounded in *Cacajao* and *Chiropotes* than in other atelids. The patellar groove decreases in relative width in *Ateles* (but is still wider than in other platyrrhines except *Callicebus*) and is broadest in *Pithecia*.

The inclusion of *Pithecia* in atelids results in a different pattern of homoplasy, as shown by Ford (1986) for a longer list of traits, and displayed here as parallelisms (Fig. 6). The derived states for five parallelisms among atelids (in addition to 24:1 between *Cacajao* and *Alouatta*) do not arise in any other platyrrhine, and all occurred only once in

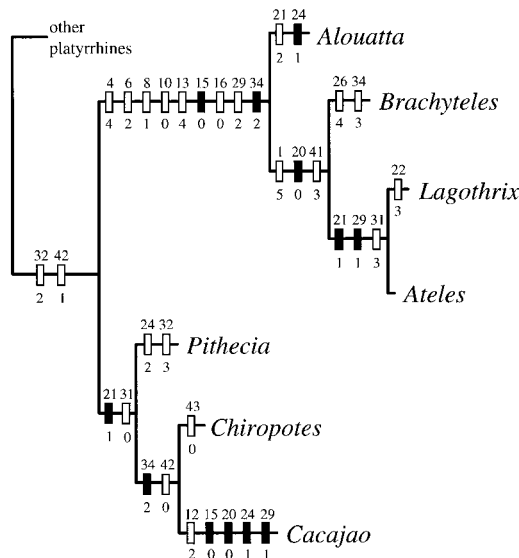


Fig. 6. Occurrence of character states unique to Ford's (1986) atelids mapped onto Ford's phylogenetic tree. Dark blocks indicate homoplastic changes. Character number is listed above, state number below.

the unrooted network. Two of these traits occur in *Cacajao* and some or all atelines: the flattened anterior border of the trochlear facet on the tibia (15:0) and the lack of subchondral bone lateral to the margin of the patellar groove (29:1,2). In addition, *Cacajao* shares with atelines (*Ateles*, *Brachyteles*, *Lagothrix*) little to no extension of the femoral head articular surface onto the neck (20:0), a reversal to the primitive condition that is unique to this clade. The *Chiropotes* + *Cacajao* clade parallels atelines in the proximal projection of the femoral head (34:2), and the basal pitheciine shares a low ridge on the posterior portion of the femoral neck with the *Ateles* + *Lagothrix* clade (21:1). Although illustrated as a parallelism, it is actually ambiguous whether one of the homoplastic traits, the proximal extension of the femoral head, arose in parallel or was lost in *Pithecia*.

Composite phylogenetic tree. In the phylogeny compiled here from different lines of evidence (Fig. 7), most of the homoplastic character states can be reconstructed with some confidence to have arisen in parallel, and only the relatively broad patellar groove

(32:2) is still an atelid synapomorphy. Though the relative breadth of the patellar groove does vary within atelids (see character distribution in Table 2), it is relatively wider in these genera than in any other platyrrhines, according to Ford (1986), so the character state change that defines atelids in this case is, in a sense, a true synapomorphy.

The main differences between this tree and that of Ford (1986) are the inclusion of *Callicebus* and *Cebupithecia*. *Cebupithecia* appears to have the greater effect in this data set, even though its phylogenetic position is considered to be more secure. As noted by Ford (1990) and Meldrum (1993), its skeleton combines a mosaic of primitive and derived features that, on the whole, differ from extant atelids, although its behavioral repertoire may have been similar to that of *Pithecia*. In this cladogram, the similarities between *Cebupithecia* and other atelids (mainly atelines or *Cacajao*) are mainly derived in parallel with the latter taxa. In other words, some characters reconstructed to occur once among extant atelids in either of the other trees are made homoplastic with the inclusion of *Cebupithecia* (8:1, 12:2, 16:0).

Callicebus also has an effect on the interpretation of homoplasy. It adds one instance of unique homoplasy within atelids (32:1 in parallel with *Ateles*) in addition to homoplasy in the shared, derived features that originally suggested a close relationship between *Callicebus* and *Aotus* (Ford, 1986) (not illustrated here). The position of *Callicebus* aids in the interpretation that the similarities between atelines and the *Cacajao* + *Chiropotes* clade have arisen in parallel and not simply been reversed or lost in *Pithecia*. This conclusion would be valid even if *Cebupithecia* did not exist. The positions of both *Callicebus* and *Cebupithecia* are necessary to show that the postcranial synapomorphies Ford (1986) proposed for atelids are results of parallel evolution and not ambiguous homoplasy.

Because clades within atelines are left unresolved, the derived states for each taxon are shown in Figure 7. If *Brachyteles* and *Lagothrix* are positioned as sister taxa (Schneider et al., 1993, 1996), or *Brachyteles* and *Ateles* (Rosenberger, 1979), the postcra-

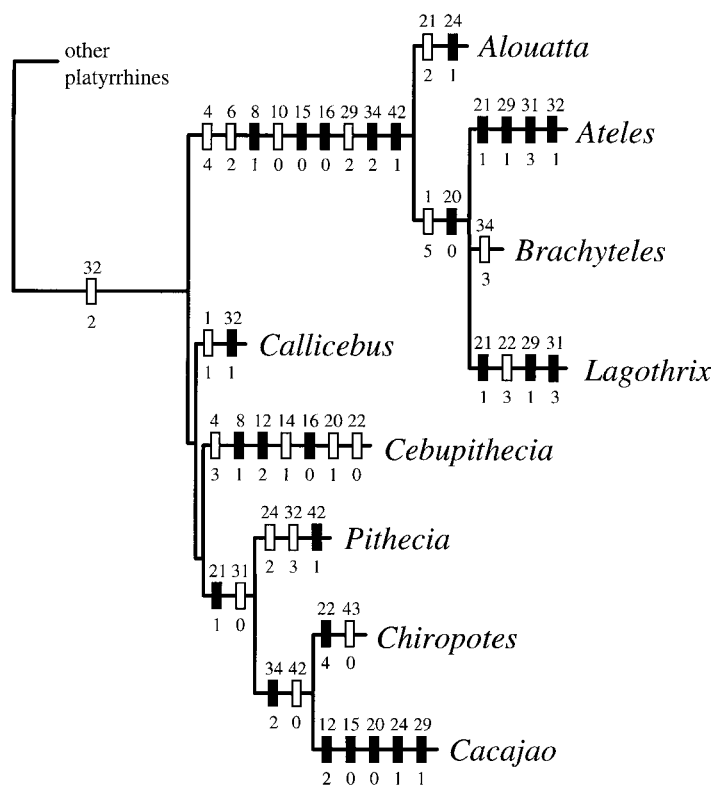


Fig. 7. Occurrence of character states unique to atelids as defined herein. Dark blocks indicate homoplastic changes. Character number is listed above, state number below. Phylogenetic tree as in Fig. 2.

nial similarities between *Ateles* and *Lagothrix* are homoplastic, but this remains uncertain.

In this phylogeny, some homoplastic traits (e.g., the proximal extension of the femoral head, reduction of the deltopectoral crest, extension of subchondral bone over the lateral lip of the patellar groove, flat anterior border of the tibial trochlear facet), are derived traits that are not only unique to atelids among platyrrhines but also rare among primates other than hominoids and *Pliopithecus*, according to the distributions in Ford (1994). All are departures from a locomotor skeleton consistent with more obligate use of quadrupedalism, and several introduce greater mobility of the hindlimb. The widened patellar groove, a potential synapomorphy of atelids, may permit a similar functional interpretation. How these characters relate to the positional behavior of atelids is discussed below.

In sum, three different phylogenetic trees have been used here to map different se-

quences of atelid character evolution. The unrooted network requires no assumptions about platyrrhine ancestral states or polarity; Ford's (1986) phylogenetic tree incorporates a rooting based on a suite of ancestral states obtained from outgroup comparisons; and a composite tree uses points of agreement among independent data sets to identify the most well-supported relationships within atelids. It can be seen that many characters that appeared to be synapomorphies of clades containing some atelids in the first two trees are identified as unique parallelisms in the composite phylogenetic tree.

DISCUSSION

The results of this study are based on the assumption that clades supported by independent data sets are more likely to be valid than are other clades. It must be recognized that the number of independent data sets applied to the question of platyrrhine phylogeny is still small (but more than for many

other primate groups). Points of agreement between two types of data, craniodental morphology and nuclear gene sequences, therefore play a significant role in the composite phylogenetic tree. This atelid phylogeny is not identical to that estimated from any single data partition, but it does have wide support (Schneider and Rosenberger, 1996; Meldrum and Kay, 1997; Horovitz and Meyer, 1997).

What follows from the use of congruence to support certain clades is that some data partitions are incongruent with aspects of the preferred tree. Probably all data partitions are incompatible in some respect with the true but unknown phylogeny. It may therefore be asked whether the incongruence is due to a pattern of homoplasy that conveys something about bias in the evolution of a particular data partition.

Patterns of homoplasy

The composite phylogenetic tree differs from the most parsimonious tree for postcranial data by incorporating into pitheciines *Cebupithecia*, a fossil taxon with a secure phylogenetic position (Kay, 1990; Kinzey, 1992; Meldrum and Kay, 1997), and *Callicebus*, a species-rich genus considered by many to be the sister group of pitheciins based on craniodental evidence (Rosenberger, 1979, 1981, 1992; Meldrum and Kay, 1997) and nuclear gene sequences (Schneider et al., 1993, 1996) or both (Horovitz and Meyer, 1997). The implications of these relationships are that few postcranial traits were involved in the most basal division between atelid groups. The ancestral atelid probably retained the morphology of generalized quadrupeds. Yet both subfamilies have progressively evolved a series of traits in parallel, several of which are not present in any other platyrrhines and some of which have also evolved in *Cebus*.

Within atelids, there are two patterns of homoplasy clearly apparent in these traits, and they interfere with phylogenetic reconstruction to different degrees. First, there is a set of traits responsible for the difference between the unrooted network and Ford's (1986) tree, which is that in the unrooted network pitheciins are paraphyletic because *Pithecia* and *Callicebus* would be omitted

using any rooting. This reflects features shared between *Cacajao* and/or *Chiropotes* and atelines, such as the relatively proximal projection of the femoral head and the form of the trochlear articular facet on the tibia. These traits are commonly inferred to be adaptations to a mobile hindlimb suitable for suspensory behavior in primates and other mammals (Fleagle, 1983; Rose, 1983; White, 1993).

While the characters shared by *Cacajao* and/or *Chiropotes* and atelines dominate homologous traits when an unrooted network is determined, these characters are recognized as homoplastic when ancestral states are incorporated into the phylogenetic reconstruction (see Ford, 1986). The knowledge that platyrrhines have an ancestor rooted in basal anthropoid primates allowed Ford (1980, 1986) to construct a plausible outgroup that yielded a rooted tree with monophyletic extant Pitheciini. Because of universal agreement on this aspect of platyrrhine phylogeny, a comparison of the unrooted and rooted trees validates Ford's approach.

Callicebus was excluded from Ford's (1986) version of atelids, and the skeleton of *Cebupithecia* suggested a more basal position than did the skull. The pattern of homoplasy that gave rise to these discrepancies is comprised of those features that appeared as synapomorphies of the ateline-pitheciin clade in Ford (1986) but are homoplastic using the definition of atelids favored here. These are the reduced deltopectoral crest and the broadened distal femur. This is not an exhaustive list, because only four bones are represented in this data set. For example, Meldrum (1993) noted that a low talar trochlea with a rounded margin is present in only extant pitheciins and atelines, so this trait falls in the same category. Meldrum (1993; Meldrum and Lemelin, 1991) also argued that the characters shared by modern atelines and pitheciines are adaptations to climbing and suspensory behaviors, but *Cebupithecia* lacks these characters and resembles other New World monkeys. Features shared by all atelids except *Cebupithecia* and *Callicebus* can be identified unambiguously as parallelisms when both of these taxa are included in atelids.

Homoplasy, positional behavior, and adaptation

To justify the adaptive importance of both patterns of homoplasy, it is necessary to incorporate data on positional behavior that was summarized in the introduction. The process of inference is shown on Figure 8, where different behavioral regimes are represented on a phylogenetic tree of platyrrhines. The behaviors of particular interest in atelids are climbing and suspension. The generalized platyrrhine condition is to emphasize quadrupedalism and minimize climbing locomotion, suspensory locomotion, or suspensory postures. Three categories of behavior are developed from this on Figure 8: 1) climbing (climbing and clambering as discussed above), 2) climbing with the additional use of hind limb and/or tail suspension in feeding behavior, and 3) climbing and suspensory postures, with the addition of forelimb/tail suspension in locomotion. Mapped onto these behavioral regimes are some examples of characters that can be argued to facilitate climbing and/or suspensory behavior.

At one level, parallel evolution is evident in adaptations to suspensory postures. The behavior that *Cacajao*, *Chiropotes*, and atelines share to the exclusion of other atelids is significant use of suspension during feeding. *Cebus* also uses tail and hind limb suspension during feeding. Different animals are thus adapted to suspensory postures in different ways and to different degrees, but that does not undermine the conclusion that the morphologies that evolve within the behavioral regime of suspension and enhance mobility in the hind limb qualify as adaptations (sensu Larson and Losos, 1996).

An analogous approach can be taken to examine the adaptive importance of the second and arguably more pervasive pattern of homoplasy: those traits that atelines and modern pitheciins share to the exclusion of *Callicebus* and other platyrrhines. Atelines and modern pitheciins show climbing and clambering locomotor behaviors that are replicated in *Cebus*, and atelins specifically incorporate suspension during locomotion. Although far from complete, the available

data on positional behavior in platyrrhines show that climbing is the only behavior that is enhanced in all of Ford's atelids relative to *Callicebus* and is the only behavior whose morphological correlates may explain why *Callicebus* is omitted from atelids when only postcranial data are considered. The evolutionary relationship of the climbing behavioral regime with homoplastic traits is illustrated on Figure 8.

The reduced deltopectoral crest and broadened distal femur can be argued to be adaptations to climbing behavior. It is unclear how to interpret the relative breadth of the patellar groove, as it is wider in atelids than in other platyrrhines, but wider still in extant pitheciins and most atelines (not *Ateles*) than it is in *Callicebus*.

In pitheciins, even the specialized *Pithecia pithecia* engages in a significant proportion of climbing (Fleagle and Mittermeier, 1980; Walker, 1996). The ranking of pitheciin taxa in this category is the same as the use of hindlimb suspension during feeding. *Cacajao* makes use of these behaviors more than do the other pitheciines, and the ranking of behavioral percentages is consistent with the distribution of parallelisms with ateline character states. It is not unexpected that adaptations to climbing and suspension may overlap, given that patterns of muscle use and bone strain are similar for these behaviors (Fleagle et al., 1981).

An intriguing observation in light of its basal phylogenetic position is that *Callicebus* spends a large proportion of its feeding time in terminal branches, as do atelines and pitheciines (Kinzey, 1976, 1981). The difference is that *Callicebus*, the smallest atelid, does not engage in below-branch behavior or climbing. However, use of the terminal branches by basal atelids similar to *Callicebus* may have been preadaptive for parallel evolution to climbing and suspensory behaviors in more derived forms. Suspensory postures are ultimately useful for enlarging the potential foraging area in terminal branches (Grand, 1972).

The homoplastic traits discussed here have broader relevance to primate evolution. One of Ford's (1994) studies from which these characters are drawn involves a much wider investigation of primate and anthropoid phy-

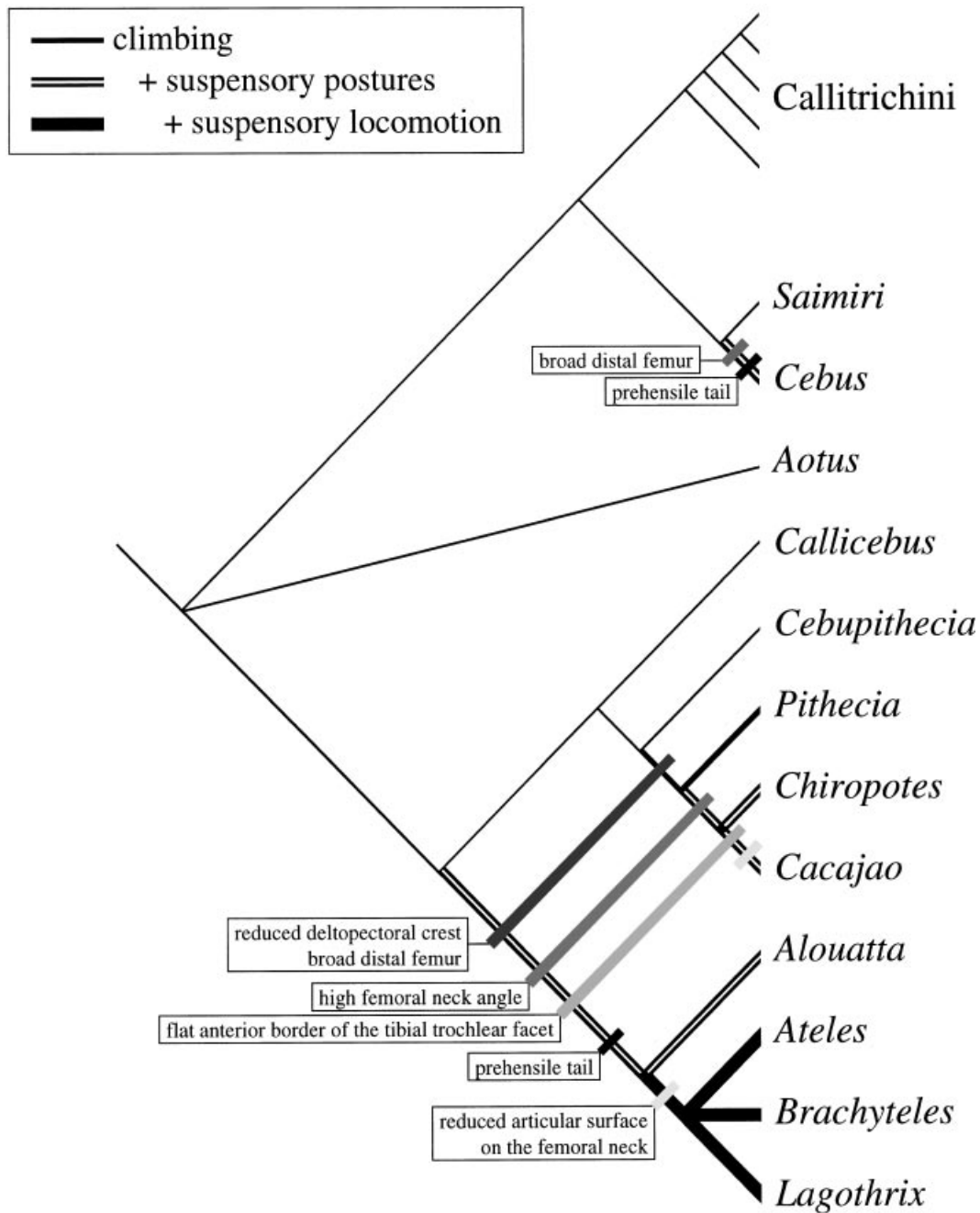


Fig. 8. Behavioral regimes and morphology superimposed on a phylogenetic tree of atelids and other platyrrhines. The behaviors indicated in the key are additive, so, for example, atelins engage in climbing, suspensory postures, and suspensory locomotion. These are not exhaustive but are illustrated because of their relationship to the homoplastic traits. Likewise, the traits mapped onto the cladogram are examples from those shown in Figures 5–7 and Table 2 and not a complete list.

logeny. An unconstrained phylogeny (Fig. 1a in Ford, 1994) shows a clade that contains pitheciins, atelines, *Pliopithecus*, and the only extant hominoids included in the analysis, *Pan* and *Hylobates*. As Ford states in the study, there are strong biogeographical reasons for concluding that this is not true. However, it serves to illustrate that some pitheciine taxa, in addition to atelines, converge upon primates generally regarded to possess a suite of postcranial adaptations related to climbing and suspensory behaviors. *Pithecia pithecia* is the odd primate out of this group, adapted to some extent to climbing postures but lacking adaptations to suspensory postures and showing autapomorphic morphology related to dramatic leaping behavior. Other species of *Pithecia* may be more generalized in their leaping behavior, though the reports thus far are preliminary (Happel, 1982; Peres, 1993). There have also been anecdotal reports of hindlimb suspension (Sanderson, 1957; Stern, 1971; Buchanan et al., 1981).

How does character selection and definition affect homoplasy?

Even if we accept the probable relationship of morphology and behavior in the patterns of homoplasy discussed here, there remain several questions about homoplasy that relate to character selection and definition. For example, it may be asked whether these homoplastic characters are independent or whether some of them are so closely linked functionally that they should be considered as a single character. Functional integration is not the case, because the characters occur in a mosaic fashion across the phylogeny, and it is clear that each of the species has a unique combination of traits just as it has a unique positional repertoire and a unique commitment to climbing and/or suspension. Strictly speaking, the characters are therefore structurally independent, even though they do represent different and perhaps successive ways of adapting to categorically similar selective pressures. Investigation of other taxa is necessary to clarify whether they typically evolve in a particular sequence.

It is also evident that these characters are broadly correlated with body size, as *Chiropotes* and particularly *Cacajao* show body

size increases independent of atelines (Ford and Davis, 1992). Because *Cebus* is of a similar body mass to these animals, it is noteworthy that it parallels the atelines and pitheciins in morphology and positional behavior more than does any other platyrrhine. Size should probably be considered as a type of constraint that originally evolved because of factors other than positional behavior (e.g., Cartmill and Milton, 1977; Fleagle and Mittermeier, 1980). The relationship between body size and suspensory behavior clearly depends on context, and platyrrhines may have a relatively low threshold above which climbing and suspensory behaviors become important (compare to the much larger-bodied hominoids).

Another possible source of homoplasy related to character selection is that most of these traits are adaptive, meaning that they have fairly clear functional roles and would be expected to respond to natural selection. This may imply that they are more prone to change than are nonadaptive or selectively neutral characters. This widespread belief is one of the reasons morphological data are thought by some to provide inherently less accurate estimates of phylogeny than molecular data (e.g., see Givnish and Sytsma, 1997). However, the premise is debatable, for a critical functional role can also be argued to constrain the rate with which a particular anatomical trait may change. Even if one does choose to favor nonadaptive morphological characters, it is not trivial to separate these from adaptive characters, and for this reason a practical alternative to using adaptive morphology in phylogenetic analysis has not been offered. Morphological data sets suitable for cladistic analysis of primate phylogeny typically involve a substantial number of adaptive characters and are therefore similar in composition to the present data set.

With respect to issues of character selection, it must be emphasized that this study is not intended to judge the general utility of postcranial data in estimates of phylogeny. In other groups, and even within this family but at lower hierarchical levels, postcranial data are very phylogenetically informative, and craniodental or other data display an abundance of parallelisms (e.g., dental homoplasy within atelines (Anthony and Kay,

1993; Horovitz and Meyer, 1997); see also Begun et al., 1997; Sanchez-Villagra and Williams, 1998). Which kinds of data partitions are important to the identification of particular clades must be investigated on a case-by-case basis.

Causal explanations

One category of biological explanations for homoplasy in the present data set is that clades possess structural and developmental limitations that may lead to the repeated evolution of particular characters (e.g., Wake, 1991). Distinguishing between developmental and ecological bases for these patterns of homoplasy is not a trivial undertaking, and these causes are not mutually exclusive. To a certain extent, similarities in developmental potential are necessary to permit selection to evoke a similar response. The question is whether a unique developmental potential can be said to characterize the atelid clade. One way to investigate this is to determine whether the homoplastic traits are truly structurally and developmentally homologous. The present study has not analyzed individual traits in a way that would allow this comparison. Still, the convergence between some atelids and hominoids (and some nonprimates) for several of these characters suggests that parallelisms within atelids do not indicate a special set of developmental constraints.

A more proximate basis for the patterns of homoplasy in atelids may be found in ecological factors unique to the South American environment. The structure of the forest canopy in South America is one explanation that has been offered by Emmons and Gentry (1983) for the proliferation of prehensile tails and gliding mechanisms in animals on this continent. Lianas are generally sparsely distributed and of poor quality, eliminating one important type of substrate for locomotion and posture. In this context suspensory behaviors may be of greater necessity, particularly in terminal branches. Emmons and Gentry (1983) applied this interpretation to prehensile tail suspension, but it may also apply to other climbing and/or suspensory behaviors of some pitheciines and atelines. This is especially pertinent given the frequent independent evolution of similar behaviors in other South American mammals

such as the margay and kinkajou, both carnivorans, and xenarthrans such as sloths and some anteaters (Emmons and Gentry, 1983; White, 1993; Meldrum et al., 1997). Thus, the patterns of homoplasy in atelids are not related to the limitations of a developmental program that itself defines the clade. Behavioral evolution in this family reflects a broader environmental bias characterizing the evolution of mammals on the continent they occupy, and morphological evolution shows a corresponding pattern.⁴

Although the critical step in identifying a bias in a particular data partition is the recognition that other lines of evidence are incongruent, the plausibility of a particular hypothesis of homoplasy should also be judged by other means and may facilitate the choice of phylogeny when there is weak congruence among independent studies (cf. Begun and Kordos, 1997). Further studies of other South American mammals, which do appear to show parallel evolution in ways similar to atelids, may provide an independent method of evaluating the hypothesis of homoplasy and adaptation that I provide above.

The co-occurrence of homoplastic traits with some behaviors highlights the problem in considering the most parsimonious cladogram for a particular data partition to be an accurate estimate of phylogeny, especially when that data partition may be heavily influenced by a single behavioral regime. In data examined here, the evolutionary pattern identified by the phylogenetic reconstruction is the adaptation to various forms of positional behavior. Whether this reveals a hierarchy that is coincident with the true order of speciation events is a question that must be addressed with respect to other types of data. In this case, several patterns of adaptation are shown to be homoplastic.

There is no reason to doubt that other data partitions, such as the skull, show patterns of homoplasy in an analogous fashion but are influenced by other selective pressures. While different kinds of morphological data are probably informative regarding different aspects of phylogeny, there is presently no way to predict the phylogenetic

⁴Similar logic was the basis for Begun's (1993) explanation of convergence in hominoid phalangeal morphology, which appears to be ecologically driven.

information content of a data partition. This reaffirms the common conclusion that numerous lines of evidence should be brought to bear on phylogenetic reconstruction. Beyond this, the analysis of homoplasy can provide additional information on how biases in development or environment play a role in directing the course of evolution within particular data partitions. In a sense, therefore, homoplasy is as meaningful as the phylogeny itself.

SUMMARY

In sum, the atelid postcranium can be seen as a data partition in which parallel selection has led to patterns of homoplasy that interfere to some degree with phylogenetic inference concerning the membership of the family and its component subfamilies. The strongest signal in character distributions for the atelid femur, tibia, calcaneus, and humerus is one of adaptation to some use of climbing locomotion. These traits overwhelm homologous traits in the reconstruction of phylogeny, and taxa that rarely engage in these behaviors are omitted from the atelid clade when data outside the postcranium are not examined. In a more restricted set of taxa, suspensory adaptations evolve in parallel, mainly in the hindlimb.

Several of the traits demonstrated to be homoplastic within atelids are also found in some or all hominoids as well as other South American mammals, suggesting that these parallelisms do not have a basis in developmental or structural constraints peculiar to atelids. Instead, aspects of canopy structure in South America may introduce a bias toward selection for climbing and suspensory behavior in relatively large-bodied mammals. This example emphasizes that data partitions strongly influenced by a particular behavioral regime (in this case, aspects of positional behavior) cannot be assumed to have a phylogenetic signal ascertainable through parsimony-based analyses.

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APPENDIX. Character state descriptions¹

Calcaneus

1. PC4, A2: Location of the peroneal tubercle: 1, on anterior half but posterior to anterior end; 2, polymorphic for states 1,3; 3, approximately centered; 4, polymorphic for states 3,5; 5, on posterior half
2. PC6, A3: Position of anterior articular facet for the astragalus (on anterior sustentaculum): 0, anterior articular surface extends broadly to anterior end of bone; 1, polymorphic for states 0,2; 2, does not reach anterior end
3. PC7, A4: Connection between anterior and medial articular (sustentacular) facets: 0, anterior and medial articular surfaces separate; 1, polymorphic for states 0,2; 2, articular surfaces confluent
4. PC10/12, A5: Degree of concavity of cuboid articular facet: 0, flat articular surface; 1, slightly concave; 2, moderately concave; 3, deeply concave; 4, concave superomedially, convex lateroplantarly
5. PC19, A6: Navicular articular facet: 0, absent; 1, polymorphic for states 0,2; 2, present
6. PC26, A7: Tuber calcanei: 0, small and indistinct; 1, moderately large; 2, very large
7. PC29/30, (A52): Length of peroneal tubercle relative to maximum length of calcaneus: 0, mean greater than 0.30; 1, mean less than 0.30
8. PC33, (A9): Length of posterior articular surface relative to maximum length of calcaneus: 0, less than 0.38; 1, greater than 0.38
9. PC36, A53: Ratio of width to length of posterior articular facet for the astragalus: 0, mean less than 0.59; 1, mean greater than 0.59

Tibia

10. PC40/41, A11: Shape of distal shaft: 0, anteromedial edge extremely rounded; 1, triangular in cross section; 2, lateral edge rounded
11. PC43, A12: Anteroposterior length of distal facet for the fibula: 1, moderately long facet; 2, long facet
12. PC45, A13: Proximodistal depth of distal facet for the fibula: 0, shallow or absent facet; 1, polymorphic for states 0,2; 2, medium depth facet; 3, polymorphic for states 2,4; 4, deep facet
13. PC46, A14: Position of distal facet for the fibula: 0, anterior location of face or absent; 1, central location; 2, polymorphic for states 1,3; 3, posterior displacement of facet; 4, anterior portion curves out, faces posteriorly
14. PC50, A15: Posterior border of trochlear facet for astragalus: 0, flat; 1, rounded; 2, polymorphic for states 1,3; 3, sharp
15. PC51, A16: Anterior border of trochlear facet for astragalus: 0, flat; 1, sharp
16. PC52, A17: Squatting facet on anterior face of distal tibia: 0, no trochlear facet extension onto the anterior shaft; 1, slight anterior extension; 2, polymorphic for states 1,3; 3, moderate anterior extension; 4, large anterior extension

APPENDIX. (continued)

17. PC54, A18: Horizontal groove on posterior malleolus: 0, absent; 1, polymorphic for states absent and slight groove; 2, marked groove
 18. PC56, A19: Ratio of depth (AP) to breadth (ML) of trochlear facet for astragalus: 0, mean greater than 1.10; 1, 1.00–1.10; 2, less than 1.00
 19. PC60/61, (A20): Ratio of medial malleolar height to the mediolateral length of the trochlear facet: 0, mean less than 0.57; 1, 0.57–0.70; 2, mean greater than 0.70
- Femur
20. PC67, A21: Extension of head onto posterior neck: 0, slight or no extension; 1, moderate extension; 2, polymorphic for states 1,3; 3, superoposterior extension of head which merges imperceptibly into neck
 21. PC71, A22: Presence of ridge on posterior neck: 0, absent (flat posterior surface of neck); 1, polymorphic for states 0,2; 2, low rounded mound; 3, polymorphic for states 2,4; 4, distinct ridge
 22. PC72, A23: Intertrochanteric crest: 0, absent below trochanteric fossa; 1, polymorphic for states 0,2; 2, crest extends distally beyond trochanteric fossa but does not turn medial; 3, indistinct or faint crest to lesser trochanter; 4, polymorphic for states 3,5; 5, distinct crest extending to lesser trochanter
 23. PC74/75, A24: Position of lesser trochanter: 0, slightly medial; 1, posteromedial; 2, slightly posterior
 24. PC76, A25: Shape of smooth (subchondral) bone on lesser trochanter: 0, round; 1, fat oval; 2, oval; 3, polymorphic for states 2,4; 4, long and thin
 25. PC78, A26: Anterior bowing of shaft: 0, straight; 1, polymorphic for states 0,2; 2, slight anterior bow
 26. PC79, A27: Third trochanter: 0, present and distinct; 1, polymorphic for states 0,2; 2, slight rise or roughened area; 3, polymorphic for states 2,4; 4, absent
 27. PC83/84, A28: Depth of patellar groove: 0, very shallow to flat; 1, shallow; 2, moderate; 3, deep
 28. PC85, A29: Shape of lateral margin of patellar groove: 0, rounded; 1, moderately sharp; 2, sharp
 29. PC86, A30: Extension of subchondral bone beyond lateral margin of patellar groove: 0, facet surface of patellar groove curls over lateral border onto lateral surface; 1, polymorphic for states 0,2; 2, no curl over lateral edge
 30. PC89, A31: Ratio of neck diameter relative to mediolateral proximal shaft diameter (PSTD): 0, mean greater than 1.01; 1, 0.93–1.01; 2, less than 0.93
 31. PC93/94, A33: Position of third trochanter, measured as ratio of length from greater trochanter to top of third trochanter relative to lateral length of femur: 0, mean less than 0.10; 1, 0.10–0.14; 2, 0.15–0.17; 3, greater than 0.17
 32. PC95, (A34): Ratio of patellar groove width relative to mediolateral width of the distal epiphysis: 0, mean less than 0.46; 1, 0.46–0.47; 2, 0.48–0.53; 3, greater than 0.53
 33. PC96, A35: Ratio of distal epiphysis depth (AP) relative to biepicondylar breadth: 0, mean greater than 0.83; 1, mean less than 0.83
 34. PC97/98, A36: Ratio of proximal head projection relative to greater trochanter projection: 0, mean less than 0.87; 1, 0.88–1.14; 2, greater than 1.14
 35. PC99, A37: Lesser trochanter projection relative to PSTD: 0, mean greater than 0.80; 1, 0.75–0.80; 2, less than 0.75

APPENDIX. (continued)

Humerus

36. PC104, A39: Presence of epicondylar foramen: 0, present; 1, polymorphic for states 0,2; 2, absent
37. PC106, A40: Trochleocapitular ridge: 1, rounded and slightly distinct; 2, rounded and moderately distinct; 3, polymorphic for states 2,4; 4, rounded and very distinct; 5, polymorphic for states 4,6; 6, sharp, distinct ridge
38. PC107, A46: Dorsal displacement of medial epicondyle: 0, no displacement (parallel to long axis of trochlea); 1, polymorphic for states 0,2; 2, slight displacement; 3, polymorphic for states 2,4; 4, large degree of displacement
39. PC108, A41: Supinator crest: 0, wide crest; 1, moderately wide; 2, polymorphic for states 1,3; 3, slightly rounded
40. PC112/113, A42: Shape of ventral trochlea: 0, cylinder- or spool-shaped; 1, cone- or spool-shaped; 2, cone-shaped; 3, cone- or cylinder-shaped; 4, cylinder-shaped
41. PC116, A43: Bicipital groove: 0, shallow and wide; 1, polymorphic for states 1,2; 2, moderately deep and wide; 3, deep and narrow
42. PC117/118, A44: Shape of deltopectoral crest: 0, very rounded, shaft quite smooth; 1, rounded; 2, flattens superiorly; 3, polymorphic for states 2,4; 4, intermediate crest, shaft flattened into long, thin triangle
43. PC130/131, A47: Ratio of minimum trochlear diameter (anteroposterior) relative to maximum trochlear diameter: 0, mean less than 0.72; 1, mean between 0.72 and 0.82; 2, mean greater than 0.82

¹ Adapted from Ford (1986, 1994). To facilitate comparison with these previous studies, Ford's abbreviations are given in addition to the character number used here. PC refers to Ford (1986); A refers to Ford (1994). In some cases, parentheses indicate that the character used by Ford (1994) has no direct homologue in Ford (1986) but intends to express the same morphology. A slash indicates that characters from Ford (1986) were combined. Where one of the combined characters was nonvariant in platyrrhines according to Ford (1986), that character is not indicated.

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